

STRUCTURES OF THE FEMALE REPRODUCTIVE SYSTEMS IN PANORPIDAE (MECOPTERA) WITH REMARKS ON THEIR TAXONOMIC SIGNIFICANCE

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Abstract The female reproductive systems vary prominently among six Chinese species in the family Panorpidae, notably in the number of ovarioles, the color of spermathecal membrane, the size of accessory glands, and the relative position of each other. The ovaries are of polytrophic type. There are 10 ovarioles in each ovary in *Panorpa longihypovalva* Hua et Cai and *Necpanorpa lui* Chou et Ran, 16 ovarioles in *P. magna* Chou, 18 in *P. obtusa* Cheng, and 28 ovarioles in *P. tincta* Navás. *P. changbaishana* Hua generally possesses 8 ovarioles in one ovary and 10 in the other, showing asymmetry in a same individual. The spermathecal membrane is red in *P. changbaishana* Hua, but transparent in others. The accessory glands of *P. magna* are the largest among the six species, almost as thick as its ovary. We concluded that the female reproductive systems are useful in species determination in Panorpidae, and the phylogenetic relationships of Mecoptera are briefly discussed. Besides, *Panorpa changbaishana* Hua is a new name proposed for *Panorpa choui* Hua, 1998.

Key words Mecoptera, Panorpa, Necpanorpa, ovary, spermatheca, phylogeny.

The Mecoptera is a small order in Hexapoda, comprising only about 600 extant known species in 9 families (Penny & Byers, 1979; Penny, 1997). As their unique position in the phylogeny of Holometabola, Mecoptera have drawn much more attention out of proportion to their small numbers (Byers & Thornhill, 1983). In recent years, phylogenetic studies based on molecular data (Whiting, 2002) and on the ovary structural data in the snow scorpionflies (Šys & Bili ski, 1990; Bili ski & B üning, 1998; Bili ski et al., 1998) and in Nannochoristidae (Simiczyjew, 2002) suggested that the Mecoptera might be paraphyletic with Boreidae as a sister group to Siphonaptera. A study on sperm structure, however, reached somewhat contradictory conclusion and support the traditional view of the monophyly of Mecoptera (Dallai et al., 2003). In the family Panorpidae, using the mitochondrial gene evidence, Misof et al. (2000) found that the genus *Panorpa* is most likely paraphyletic to the genus *Necpanorpa*. Our recent fauna investigation also proved that the genus *Panorpa* is a very heterogenous group and may need to be further subdivided (unpublished data). In contrast to the keen interest on the relationships to other orders, the Mecoptera studies thus far mainly concentrate on the taxonomy at species level, and the internal anatomy research is considerably rare. Potter (1938) described and illustrated the digestive, nervous and reproductive systems of 7 species of mecopterans in 5 families, and made a comparison among families.

Simiczyjew (2002, 2003a, 2003b) analyzed the ovarian structures of Nannochoristidae, Bittacidae, and Panorpididae, and discussed the phylogenetic relationship from oogenesis perspective. Most reproductive system researches, however, were on the family level, not on the generic level, let alone on the specific level. Recently, we reported the female reproductive system of *Panorpa lui* Hua (Hou & Hua, 2007). No investigations have yet been made on the interspecific differences of female reproductive organs in scorpionflies to date. In order to elucidate if the internal female reproductive organs can be used to distinguish scorpionfly species, we chose six representatives of scorpionflies to make a comparative study on their female reproductive systems.

1 Materials and Methods

Female adults of *Panorpa changbaishana* Hua were collected on the 25th July 2006 at the Peace Forest Farm along Erdaobaihe River, Jilin Province. *P. longihypovalva* Hua et Cai, 2008, *P. magna* Chou, 1981, and *P. obtusa* Cheng, 1949 were collected on the 26th June 2006 from the Honggou Forest Farm, about 20 km south of Taibai County, Shaanxi Province. The females of *P. tincta* Navás, 1931 were collected on 18th July 2004 from the Huoditang Forest Farm in Ningshan County, Shaanxi Province. *Necpanorpa lui* Chou et Ran, 1981 were collected on the 7th July 2005 from Liping National Forest Park in Nanzheng County, Shaanxi Province. All freshly

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collected living specimens were fixed in a mixture of ethanol and acetic acid (3 : 1 v/v) for 12 h, then preserved in 70 % ethanol at 4 °C.

After legs and wings were cut off, the adults were put into Petri dishes filled with some water. The integument was decorticated with forceps and needle from tergum to sternum. Finally, the alimentary canal was eliminated, and the whole reproductive system was observed and figured under Nikon SMZ 1500 microscopes and Nikon Eclipse50i, and photographed using Nikon CoolPix5000 digital camera.

2 Results

2.1 General structure of the female reproductive organs

The insect reproductive system generally contains two parts, the external genitalia and the inner reproductive organs. The female genitalia of scorpionflies consist of an internal skeleton and a subgenital plate. The female inner reproductive organs include a pair of ovaries, two lateral oviducts, a common oviduct, a pair of accessory glands with their duct, and a spermatheca with spermathecal duct. The ovaries consist of a series of ovarioles generally lying dorsolateral to the alimentary canal. The two lateral oviducts unite along the medial line of the body with the common oviduct, which extends to the ninth abdominal segment and opens into the genital chamber formed by the subgenital plate and the internal skeleton. Two accessory glands lie in the ventral to the alimentary canal, merging to form a common duct at the sixth or seventh abdominal segment. The spermatheca, whose shape has little differentiation among species, generally lies on the ventral side of the common oviduct opening between the axes of internal skeleton. The apex of the spermatheca bends posteriorly in 7-shaped. The membrane of spermatheca is thin and transparent in most part, but thick and opaque in the basal 1/3. The ducts of spermatheca, accessory glands, and common oviduct each ends at the ninth segment, all opening into the genital chamber independently. The duct of accessory glands is in dorsal position, the common oviduct ventral, and the spermathecal duct in the middle.

2.2 Specific descriptions of the female reproductive organs

2.2.1 *Panorpa longihypovalva* Hua et Cai (Fig. 1)

The reproductive organs are situated between the third and ninth abdominal segments. The ovaries lie on the dorsal part of the third to sixth segments; each ovary generally consists of 10, sometimes 9 or 11 ovarioles. The ovarioles are long, usually arising from a straight line along oviducts. The apices of ovarioles point to the dorsal midline, and two ovaries integrate closely. The two lateral oviducts lie on the outer side of the ovaries

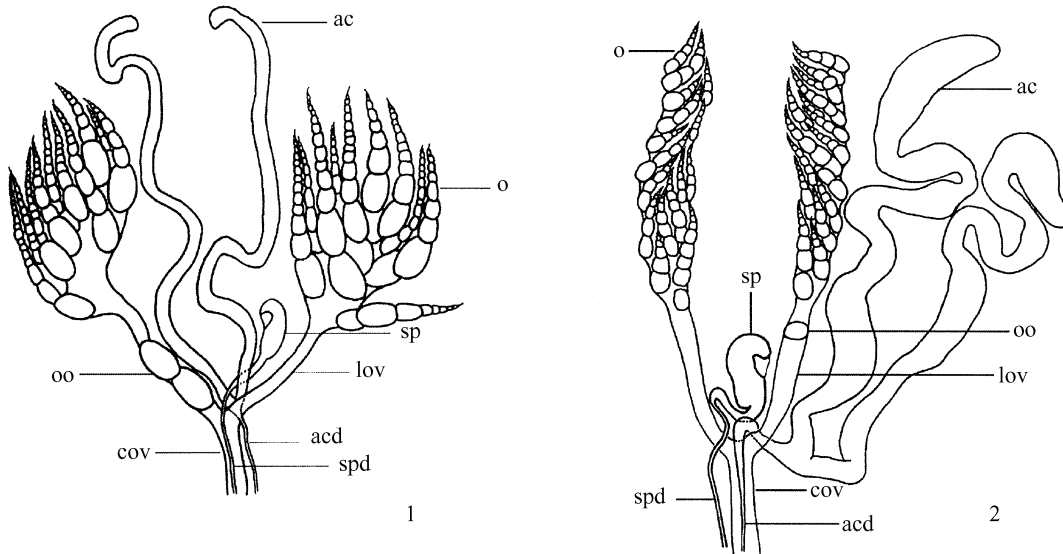
and unite with the common oviduct along midline in the sixth abdominal segment. The accessory glands extend forwards into the third abdominal segment and unite in the posterior region of sixth segment to form a duct. The anterior region of accessory glands is relatively unfold and mainly coiled in the fifth to sixth abdominal segments. The duct is much thinner than accessory glands themselves, usually trespass laterally from the right side of the lateral oviducts to the dorsal side of the common oviduct, eventually opening into the genital chamber. The bean-like spermatheca has transparent membrane, being located between the accessory glands in the ventral side of the sixth abdominal segment. The spermathecal duct crosses consecutively between the two accessory glands and between the lateral oviducts, then running along the dorsal surface of the common oviduct, and finally linking with the internal skeleton.

2.2.2 *Panorpa magna* Chou (Fig. 2)

Panorpa magna differs greatly with other species in the female reproductive systems. The reproductive organs occupy the whole abdomen, from the first until ninth segments. The ovaries, which are relatively small, lie on the dorsal part of the first to forth or fifth abdominal segments. Each ovary usually consists of 16 to 18 ovarioles, with 16 the most frequent. The ovarioles are short, growing opposable on the lateral oviduct. Not as in other species, the two ovaries are separated along the body midline. Fig.2 shows the natural position of the ovaries. The long lateral oviducts unite to form the common oviduct at the sixth abdominal segment. There are two bulges on the basal part of the lateral oviducts near the common oviduct. The accessory glands are peculiar for their extraordinary thickness and unevenness in diameter, nearly as thick as the ovaries. The accessory glands extend into the anterior part of the first abdominal segment, usually coiling considerably in the first and second segments, and uniting to form the common duct at the seventh abdominal segment. The duct of accessory glands generally crosses between the two lateral oviducts dorsad to run along the dorsal side of the common oviduct, L-shaped from the lateral view. The spermatheca lies in the sixth abdominal segment between the accessory glands and the lateral oviducts, but very close to the sternum and looks like a bean with transparent membrane. The spermathecal duct runs laterally from the left side to the dorsal part of the common oviduct in the seventh abdominal segment, eventually linked with the internal skeleton.

2.2.3 *Panorpa obtusa* Cheng (Fig. 3)

The reproductive organs also occupy the whole length of abdomen, extending from the first to the ninth segments. The ovaries are situated on the dorsal part of the second to fifth abdominal segments. Each ovary consists of 18 short ovarioles, which are borne along the lateral oviducts and extend to the midline. The two



Figs. 1-2. Female reproductive organs, dorsal view. 1. *Panorpa longihypovalva*. 2. *P. magna*. ac, accessory gland; acd, accessory gland duct; cov, common oviduct; lov, lateral oviduct; o, ovariole; oo, oocyte; sp, spermatheca; spd, spermathecal duct.

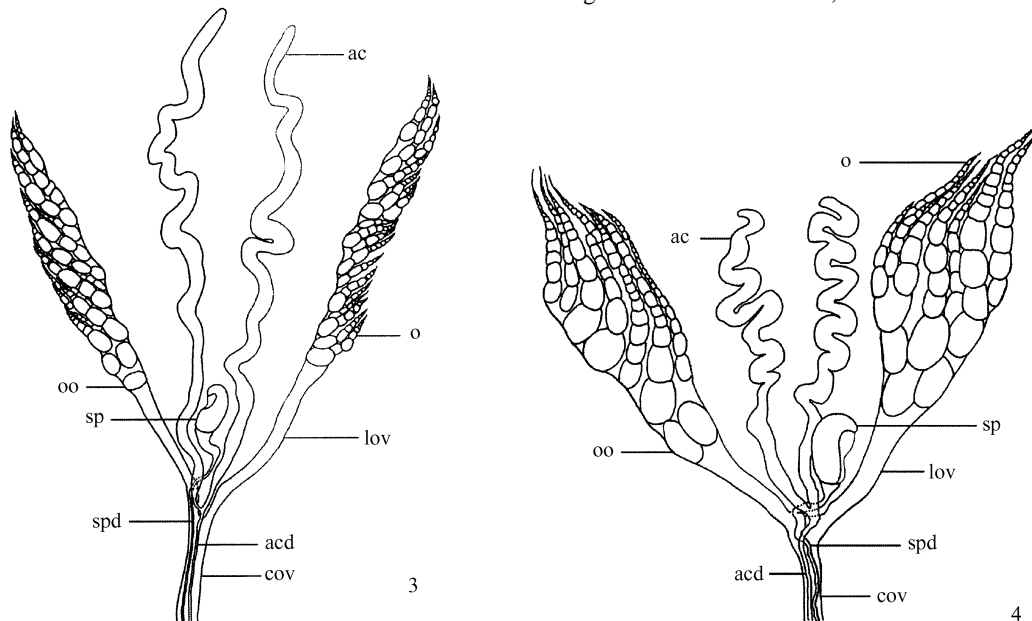
lateral oviducts are quite long, uniting with the common oviduct in the posterior part of the seventh abdominal segment. Two greatly-coiled accessory glands extend into the first abdominal segment forward and cross between the two lateral oviducts dorsad to merge into the common duct in the seventh segment backward. The position of murgence is slightly above the onset of the common oviducts, differing from that of all the other three species, in which the accessory glands usually cross between the lateral oviducts from ventral to dorsal after they merge into the common duct. The spermatheca is

located in the anterior ventral part of the sixth abdominal segment, also bean-like with transparent membrane. The spermathecal duct runs to the dorsal part of the common oviduct between the accessory glands and the lateral oviducts in the seventh segment, eventually linked with the internal skeleton.

2.2.4 *Panorpa changbaishana* nom. nov. (Fig. 4)

Panorpa choui Hua, 1998. *Entomotaxonomia*, 20 (1): 37. nom. nov.
(Preoccupied by *Panorpa choui* Zhou et Wu, 1993. *J. Zhejiang For. Coll.*, 10 (2): 190).

The reproductive organs also occupy the whole length of the abdomen, from the first to the ninth



Figs. 3-4. Female reproductive organs, dorsal view. 3. *Panorpa obtusa*. 4. *P. changbaishana*. ac, accessory gland; acd, accessory gland duct; cov, common oviduct; lov, lateral oviduct; o, ovariole; oo, oocyte; sp, spermatheca; spd, spermathecal duct.

segments. The ovaries lie on the dorsal part from the first to the sixth abdominal segments. The two ovaries are usually unsymmetrical in the number of ovarioles in the same individuals, having combinations of $11 + 9$, $8 + 10$, and $10 + 10$ in different individuals, respectively, with $8 + 10$ the most frequent. The ovarioles are long, being borne alternatively on both sides of the lateral oviduct. The two lateral oviducts unite with the common oviduct in the posterior region of the sixth abdominal segment. Two severely-coiled accessory glands extend into the second abdominal segment anteriorly and unite to form a duct in the same position with union of the lateral oviducts posteriorly. The spermatheca lies in the anterior ventral region of the sixth abdominal segment. It resembles other species in shape, but with the membrane blood red in colour and delicate in texture, so readily being broken and peeled off. The spermathecal duct runs to the dorsum of the common oviduct from the ventral side of accessory glands and link with the internal skeleton.

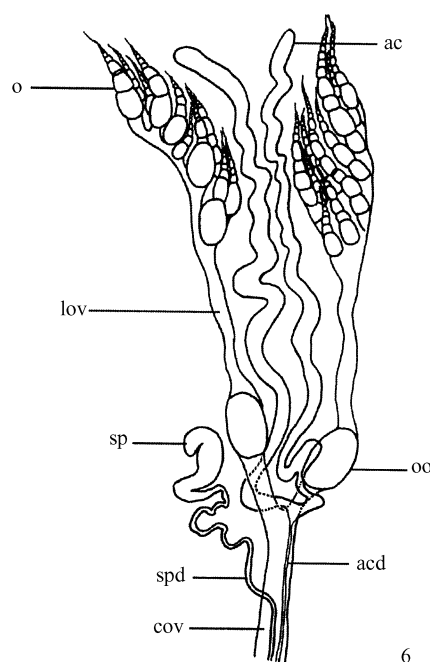
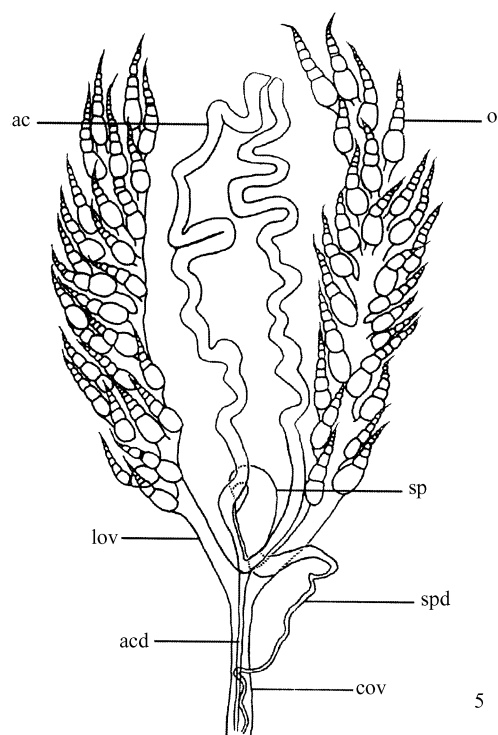
2.2.5 *Panorpa tincta* Navas (Fig. 5)

The reproductive organs of *P. tincta* Navas are situated between the third and ninth abdominal segments. The ovaries are relatively small and lie on the dorsal part of the third to sixth abdominal segments. The ovarioles, whose number is maximal in these 6 species, generally ranges from 26 to 28, with 28 the most frequent. The two short lateral oviducts unite with the common oviduct in the sixth abdominal segment. The coiled accessory glands, which lie on the ventral part of abdomen, extend

forwards into the anterior region of the third abdominal segment and unite in the sixth segment to form a common duct. The duct of accessory glands crosses between the two lateral oviducts into the dorsal side of the common oviduct. The ivory-white spermatheca is located in the sixth abdominal segment. The tip of the spermatheca bends backwards and looks thick from the color. The spermathecal ducts cross between the lateral oviducts in the sixth segment, then runs along the dorsal surface of the common oviduct, and finally links with the internal skeleton.

2.2.6 *Neopanorpa lui* Chou & Ran (Fig. 6)

The reproductive organs lie in the third to ninth abdominal segments. The two symmetrical ovaries are relatively small and situated between the third to fifth abdominal segments. Each ovary consists of 10 ovarioles. There situated lateral oviducts, part of accessory glands and spermatheca in the sixth abdominal segment. The two lateral oviducts are extremely long and unite into the common oviduct in the sixth abdominal segment. The accessory glands extend into the third abdominal segment and unite into a duct in the sixth segment. Not as in *Panorpa*, *N. lui* possesses the accessory glands near the lateral side of abdomen, being much forward than the tip of ovarioles. The duct of accessory glands runs between the two lateral oviducts to the dorsal surface of the common oviduct. The spermatheca is situated in the sixth abdominal segment, with nearly the half being bent backward. The spermatheca looks like a bean with transparent membrane. The spermathecal duct coils in



Figs. 5-6. Female reproductive organs, dorsal view. 5. *Panorpa tincta*. 6. *Neopanorpa lui*. ac, accessory gland; acd, accessory gland duct; cov, common oviduct; lov, lateral oviduct; o, ovariole; oo, oocyte; sp, spermatheca; spd, spermathecal duct.

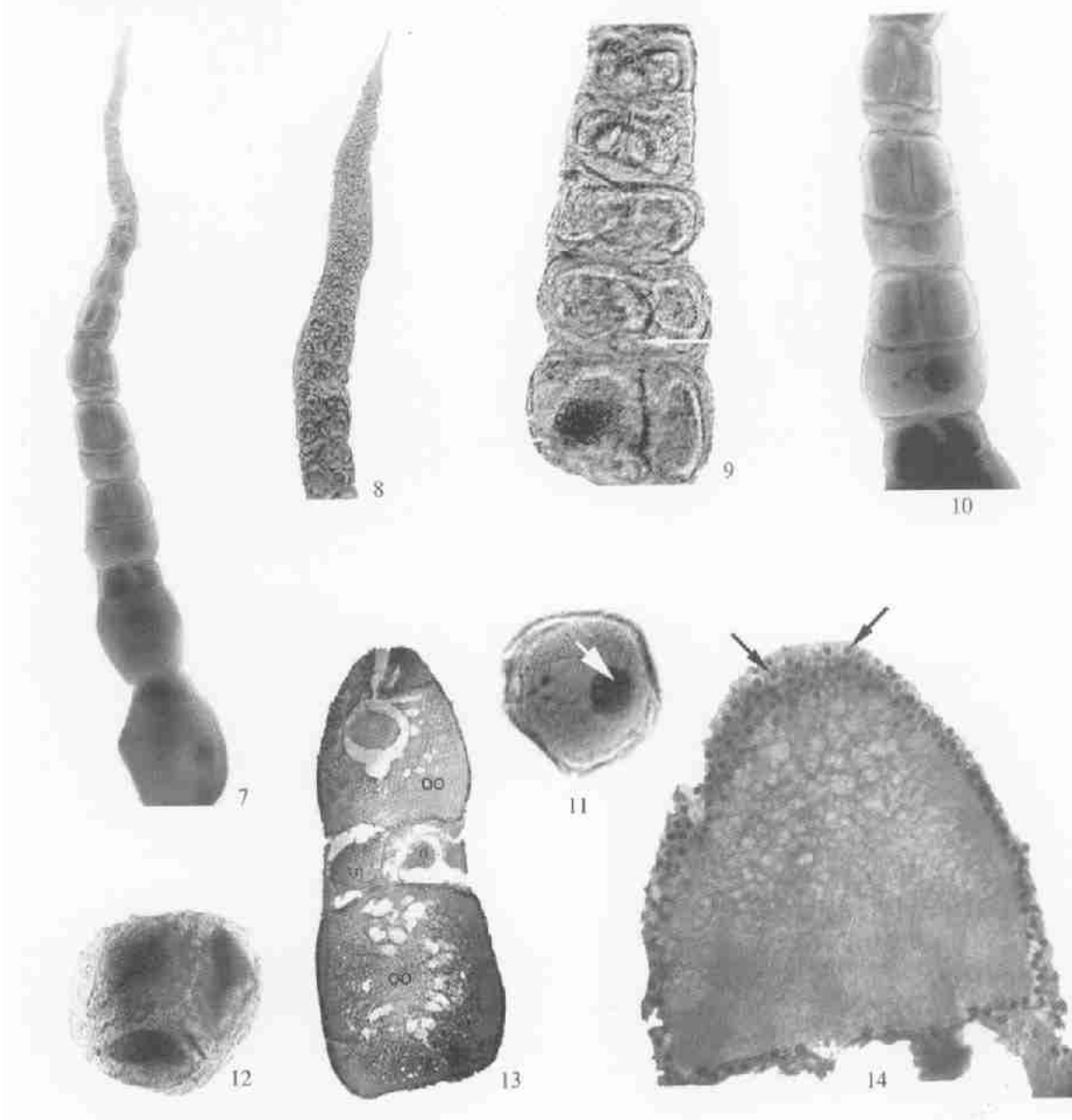
the sixth segment in most and crosses between the oviducts to link with the internal skeleton.

2.3 Structure of the ovarioles (Figs. 7-21)

The ovarioles are of polytrophic type in the genus *Panorpa*, being divided into a terminal filament, a germarium, a vitellarium, and an ovariole pedicel. The terminal filament is extremely thin, lying on the distal part of the ovary. The germarium is a place where cell division is flourishing. Oogonia divide into cystocytes, only one of the four cells within a cystocyte differentiates into the oocyte; the remaining three cystocytes develop into nurse cells or trophocytes. In vitellarium, the nurse cells provide nutrition for the developing oocytes. Along

with the maturity of the oocytes, the oocytes gradually grow larger in size, and the nutritive chamber diminishes correspondingly in size until the nurse cells vanish.

In *P. longihypovalva* (Figs. 7-14), the ovarioles are long. We could easily distinguish the oocytes and nurse cells. The terminal filament is relatively short, usually absent in mature ovaries. The germarium is also short, in which we could clearly recognize the cystocytes. The vitellarium occupies most of the ovariole and generally houses about 10 groups of oocyte and nurse cells. The vitellarium could be subdivided into two parts. One part near the germarium has small oocytes which form a triangle area under the nurse cells. In another part, the



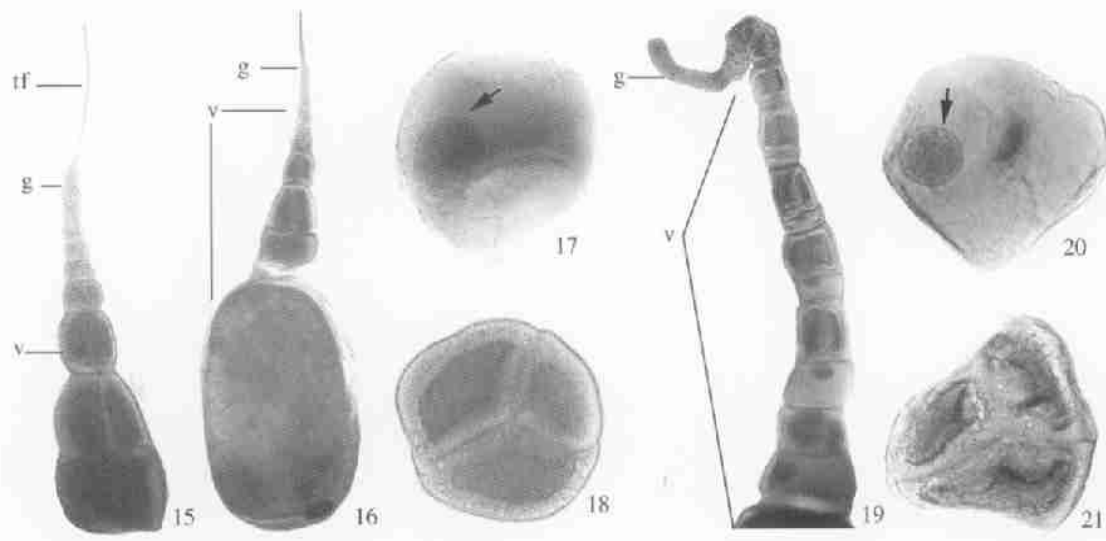
Figs. 7-14. Ovariole in *Panorpa longihypovalva*. 7. Intact ovariole. 8. Terminal filament and germarium. 9. Anterior part of vitellarium (arrow points to oocyte). 10. Vitellarium, oocytes and nurse cells arranged alternately. Along with the maturity of oocytes, the oocytes gradually grow larger, and the nutritive chamber diminishes correspondingly. 11. Oocyte in cross section (arrow shows the large nucleus). 12. Nurse cells in cross section. 13. Part of ovariole in longitudinal section, showing oocyte (oo), nucleus and nurse cell (n). 14. Oocyte in longitudinal section (arrows indicate follicle cells).

oocyte becomes much bigger and shapes into a quadrate district.

In *P. obtusa* (Figs. 15-18), the ovarioles are relatively shorter. But the terminal filament is extremely long, occupying about 1/4 to 1/3 of the whole length of the ovariole. The germarium can be easily distinguished. The vitellarium is relatively short. There are only 2 to 3 groups of oocytes and nurse cells obviously differentiated in the vitellarium.

In *P. changbaishana* (Figs. 19-21), the ovarioles are

longer. But the terminal filament is very short or almost absent, especially in the mature ovaries. Vitellarium holds a majority length of the ovariole. The oocytes and nurse cells array alternatively, the oocytes increasing gradually in size and the nurse cells decreasing in size. Generally in vitellarium there are 6 to 8 groups of extraordinarily distinct oocytes and nurse cells. This part is much longer in *P. changbaishana* than that in *P. obtusa*. This might be the main reason why the ovarioles are longer in *P. changbaishana* than those in *P. obtusa*.



Figs. 15-21. Ovarioles. 15-18. *Panopa obtusa*. 15. Ovariole, indicating the extremely long terminal filament (tf), short germarium (g), and distinct vitellarium (v). 16. Ovariole, showing vitellarium (v) composed of two or three groups of distinct oocytes and nurse cells, germarium (v) short. 17. Oocyte in cross section (arrow shows the large nucleus). 18. Nurse cells in cross section. 19-21. *P. changbaishana*. 19. Ovariole, indicating the greatly long vitellarium (v) comprised of six to eight groups of distinct oocytes and nurse cells, germarium (g) short. 20. Oocyte in cross section (arrow indicates the large nucleus). 21. Nurse cells.

3 Discussion

These scorpionflies in question differ greatly in the structures of the female reproductive organs, mainly on the number of ovarioles, the scale of accessory glands, the relative positions of various parts and so on.

Each ovary is composed of 18 ovarioles in *P. obtusa*, sixteen in *P. magna*, ten in *P. longihypovalva* and *N. lui*, and 28 ovarioles in *P. tineta*. The ovariole numbers are not universally stable among individuals, even between the both ovaries within a same specimen. In *P. changbaishana*, one ovary generally consists of 8 ovarioles and the other often 10. This situation is very similar to our former investigation on the ovarioles in *Panopa lui* Hua, which vary from 11 to 13 in number, twelve being the most frequent (Hou & Hua, 2007). Similar phenomena also occur in two European scorpionflies (Potter, 1938). *P. germanica* L. often possesses ten ovarioles in one ovary and eleven in the other, and the number of the ovarioles in *P. communis* L. was found to vary from fourteen in one ovary and twelve in the other to ten and eleven (Potter, 1938).

Nevertheless, there is generally one ovariole number that appears most frequently and being regarded as the normal number in that species. The other numbers are present roughly around the normal number. By and large, the numbers of the ovarioles in the right and the left ovary are equal in the same specimen except in *P. changbaishana*, where the ovarioles usually differ in number between the left and the right ovary in most individuals.

In the Qinling Mountains of China, there exist some species of scorpionflies with extremely similar appearances, especially their body sizes and wing markings, presenting tremendous difficulty to identification. The diagnoses rely mainly on the parameres of their male genitalia. Prior to this study, we once suspected that these so-called species might be actually the one species which show intraspecific variation among individuals. Recently, this question is solved partly as we dissected the female reproductive systems of these scorpionflies. We found that there are at least two types in female reproductive system; the number of

ovarioles is 18 in each ovary in *P. obtusa* Cheng, but there are only 13 ovarioles in each ovary in *P. nanwutaina* Chou, 1981 (unpublished data). This finding indicates that the female reproductive system, especially the number of ovarioles, might be of considerable taxonomic significance in clarifying close species of scorpionflies.

Furthermore, in *Panorpa tinctoria*, each ovary is composed of 28 ovarioles in number, much higher than other *Panorpa*, e. g. 11-13 ovarioles in *P. communis* L. (Kaltenbach, 1978), 10-14 in *P. germanica* L. (Potter, 1938). Considering other external morphology in combination, we suppose that *P. tinctoria* and other related species might merit a generic status (in preparation). For example, vein R_2 in the forewings has three branches rather than two as in *P. communis* L. (the type species of the genus *Panorpa*) and the 7th abdominal segment of male has distinct constriction at basal part and is abruptly swollen at apical two-thirds (unpublished observation).

The ovarioles also varies in lengths, being prominently longer in *P. changbaishana* and *P. longihypovalva* than in other four species. According to our investigation, the reason of their length differences is mainly due to the various length of respective vitellarium. Since the vitellarium region mainly consists of mature nurse cells and oocytes, we could conclude that the fecundity is comparatively larger in *P. changbaishana* and *P. longihypovalva* than in others.

In this paper, only one species of *Neopanorpa* is concerned. We find that although the gross structures are similar between the genus *Neopanorpa* and the genus *Panorpa*, there exists a morphological gap wide enough in the female reproductive organs to separate these two genera. In *Neopanorpa*, the lateral oviduct is extremely long, compared with short to moderately long oviduct in *Panorpa*. However, whether the ovarioles are stable in other *Neopanorpa* species needs to be further studied.

The accessory glands are a pair of thick, long, and uneven tubes in *P. magna*, being just about as thick as their ovary diameter. In contrast, the accessory glands are even, usually much thinner in others species. For the external morphology, the male *P. magna* bears two anal horns on the 6th abdominal segment, diverging markedly from other species in combination with other characters. This suggests that the female reproductive organ, especially the accessory glands, also support our erection of *P. magna* and the related species into a generic status (in preparation).

By studying female reproductive systems of Mecoptera, Potter (1938) concluded that there were differences in spermathecae among families, especially in Boreidae. The most prominent difference is the length of spermathecal duct. The spermathecal ducts of Panorpidae are generally short, but long and coiled as springs in Boreidae and Bittacidae. The spermatheca was used as an

index to differentiate species when Tjeder (1956) recorded hanging-flies of South Africa, suggesting that the spermathecae vary among species in Bittacidae. In our study, however, the spermathecae of scorpionflies are roughly the same in shape and position. There is no obvious difference except that the spermathecal membrane is blood red in *P. changbaishana*. The shapes of the spermatheca in these four *Panorpa* are similar to those in *P. communis* and *P. germanica* (Potter, 1938), suggesting that it is not advisable for the spermatheca to be used as a principal character to differentiate species.

Willmann (1987), when working on the phylogenetic relationships of Mecoptera, suggested that Nannochoristidae are the furthest clade, then are Bittacidae and Boreidae. The snow scorpionflies, Boreidae, have panoistic ovarioles, showing a close relationship with Siphonaptera (Biliński & Böhning, 1998). Nannochoristidae, represented by *Nannochorista neotropica* Navás, also have panoistic ovarioles without germarium and were deduced to be closely related with Boreidae and Siphonaptera (Simiczyjew, 2002). But Whiting (2002) and Simiczyjew (2003) proposed a sister relationship between Panorpidae and Bittacidae. From the aspect of internal female reproductive organs, both Panorpidae and Bittacidae possess polytrophic ovarioles, three nurse cells providing nutrition for one oocyte, although the length of spermathecal ducts varies from each other, whereas Boreidae and Nannochoristidae both have panoistic ovarioles. These suggest that the phylogenetic relationship of Panorpidae is much closer to Bittacidae than to Boreidae and Nannochoristidae. Since Nannochoristidae and Boreidae are closer to Siphonaptera than other mecopteran families, the conclusion above approaches Kaltenbach's (1978) phylogenetic system, which divided Mecoptera into three suborders, Eumecoptera including Bittacidae, Panorpidae, and other four families, Neomecoptera containing Boreidae only, and Protomecoptera comprising Meropeidae and Eomeropidae. The three suborder system is reasonable but putting Nannochoristidae into Eumecoptera should be further studied.

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蝎蛉科 (长翅目) 昆虫雌性生殖系统构造及其在分类学上的意义

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摘要 蝎蛉科 Panorpidae 6 种蝎蛉的雌性生殖系统间存在显著差异, 尤其是卵巢管数目、受精囊包膜颜色、附腺大小、及各部分相互间位置。卵巢管为多滋式, 每个卵巢所含卵巢管数目在长瓣蝎蛉 *Panorpa longihypovalva* Hua et Cai 和路氏新蝎蛉 *Necpanorpa lui* Chou et Ran 中为 10 根, 在大蝎蛉 *P. magna* Chou 中为 16 根, 在太白蝎蛉 *P. obtusa* Cheng 中为 18 根, 在染翅蝎蛉 *P. tincta* Navas 中有 28 根, 在长白山蝎蛉 *P.*

changbaishana nom. nov. 中, 一个卵巢一般由 8 根卵巢管组成, 而另一个经常为 10 根, 表明在同一个体中有不对称性。长白山蝎蛉的受精囊包膜为红色, 而其它种类透明。大蝎蛉附腺在 6 种蝎蛉中最大, 几乎与卵巢等粗。表明雌性生殖系统可用于蝎蛉科的种类鉴别, 并简要讨论了长翅目 Mecoptera 的系统发育关系。此外, 长白山蝎蛉 *Panorpa changbaishana* Hua 是为 *Panorpa choui* Hua, 1998 所提订的新名。

关键词 长翅目, 蝎蛉属, 新蝎蛉属, 卵巢, 受精囊, 系统发育。

中图分类号 Q964